PALAEOECOLOGY OF APPALACHIAN GYPIDULID BRACHIOPODS

by E. J. ANDERSON *and* J. H. MAKURATH

ABSTRACT. Gypidulid brachiopods lived unattached, oriented in a beak-down position aided by weighting of the posterior end of the pedicle valve. This adaptation evolved as a specialization for occupying well reworked and occasionally shifting sand substrates. This sedimentary environment characterizes the open shelf, near wave base in transgressing epeiric seas. The occurrence of *Gypidula* and its associated faunal community suggest a substrate-salinity control for the analogous *Pentamerus* Community of Ziegler.

ASSEMBLAGES of articulated gypidulid brachiopods in life position have been found in the Keyser and Coeymans Formations (Pridolian and Gedinnian) in the Appalachian Basin (text-fig. 1). These brachiopods lived in a specific orientation, on a specific substrate, and within narrowly prescribed geographical limits in Late Silurian and Early Devonian epeiric seas. This interpretation is based on two distinct kinds of evidence: (1) biologic evidence including analysis of gypidulid functional morphology and gypidulid biofacies associations, and (2) sedimentary evidence including thin-section analyses of the rocks entombing the gypidulid assemblages and mapping of vertical and lateral lithofacies patterns.

PALAEOBIOLOGIC EVIDENCE

Life position. A large slab containing *Gypidula coeymanensis* in life position was found in the Lower Devonian Coeymans Formation at Sharon Springs, New York (Pl. 39). The rock and fossil specimens were separated with a hydraulic rock splitter. The lower half of the slab and the gypidulids were then reconstructed and cemented in their original positions. Pl. 40, figs. 1–3, show views of the bottom surface of a rock slab from the Upper Silurian Keyser Formation at Hyndman, Pennsylvania. The posterior ends (beaks) of silicified specimens of *G. prognostica* are seen projecting from the naturally weathered lower bedding surface.

Two observations can be made on both the Silurian and Devonian samples: all of the obviously articulated specimens are preserved in a beak-down orientation and there is no indication of a pedicle opening in any specimen. The beak region of gypidulid pedicle valves is several times thicker than the anterior part of the pedicle valve or the brachial valve (Pl. 40, figs. 4–6). This weighting of the posterior parts of the valves served to orientate the living brachiopods all in a similar way (Ziegler *et al.* 1966), with the anterior commissure as high as possible above the substrate.

Substrate. Thin sections of the slabs containing articulated gypidulids indicate that the gypidulids lived on a substrate consisting of poorly sorted sand-sized to clay-sized skeletal fragments and relatively unbroken shells interpreted as organisms that lived at or near the sample collection point (Pl. 40, figs. 4–6). This sediment indicates an unconsolidated substrate which may have been occasionally reworked by currents, but in which most of the reworking was probably biogenic. Crude bedding and remnants of cross-stratification disrupted by burrows and mottled

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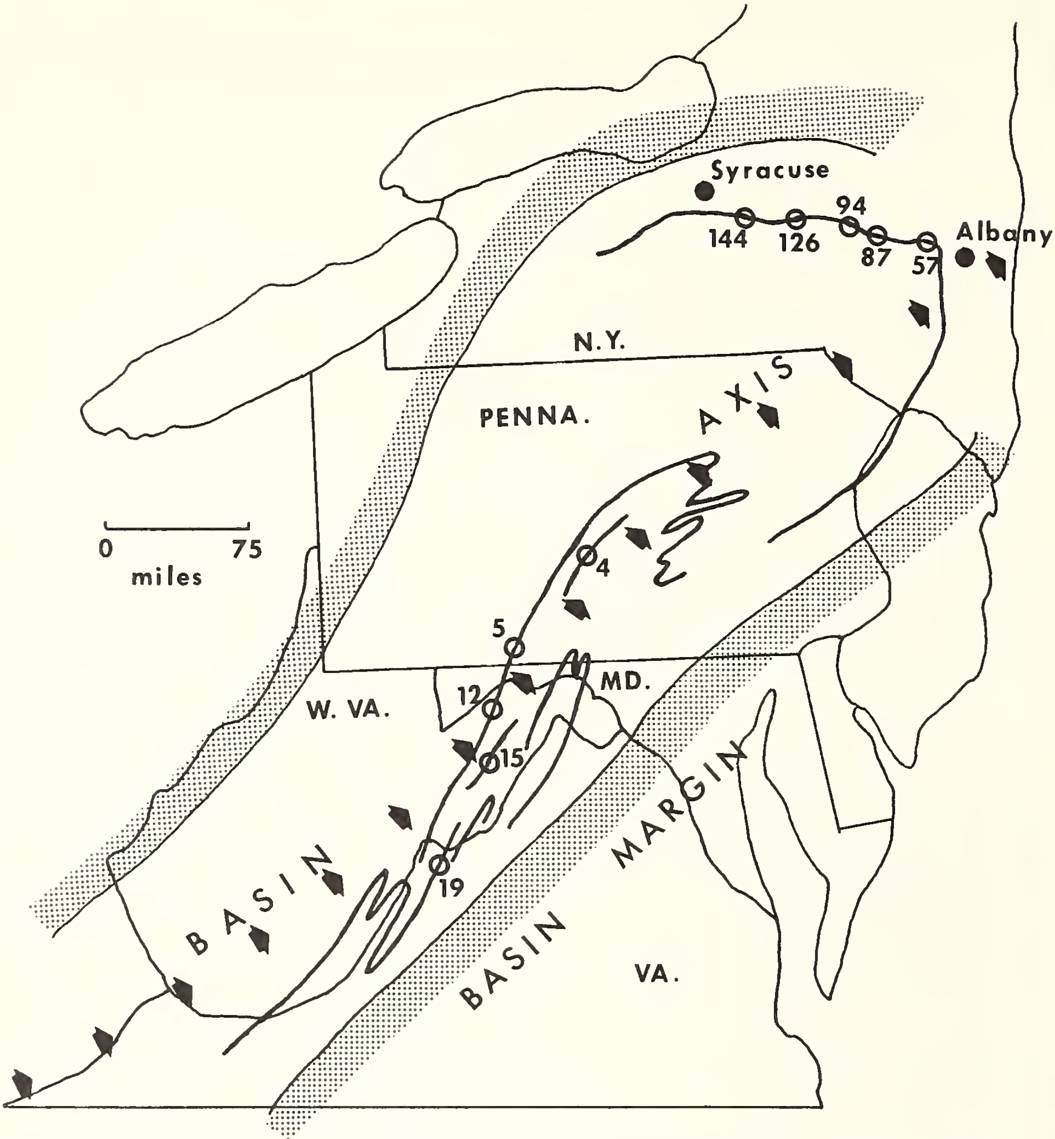

TEXT-FIG. 1. Outcrop map of the Upper Silurian and Lower Devonian in the central Appalachians. Sample localities and general configuration of the depositional basin are indicated. Arrows marking the basin axis show the general transgressive trend. New York localities are those of Rickard (1962, p. 120); other localities are described in Bowen (1967, p. 65).

EXPLANATION OF PLATE 39

Lower Devonian, Sharon Springs, N.Y. (loc. 87).

Figs. 1, 3. Front and back views of a slab showing *G. coeymanensis* in life position on its original substrate. 1, × 1·2, 3, × 1·5.

Figs. 2, 4. Front and back views of a second slab showing *G. coeymanensis* in life position, × 1.

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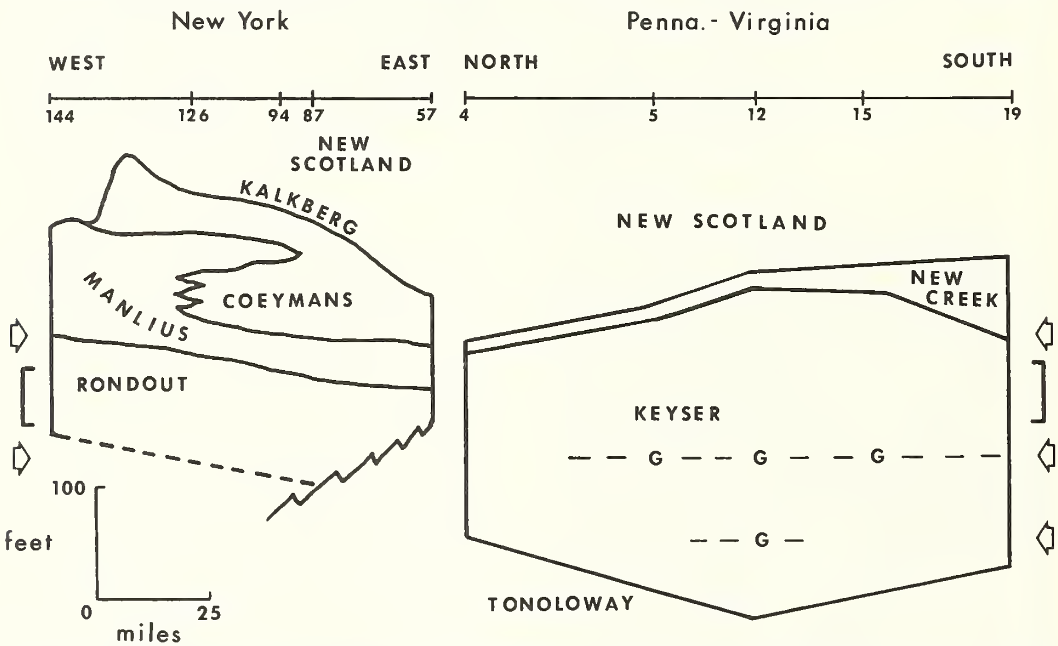
Faunal association. Gypidulids occur with a limited brachiopod fauna dominated by robust globose forms, the most common of which are atrypids and uncinulids. Ramose ectoprocts, cystoids, and crinoids are the other common faunal elements. Faunas may be expected to become more restricted in higher-energy zones nearer shore, whereas more diverse brachiopod faunas dominated by a mixture of large flat and small angular forms are more characteristic of silt and clay substrates further offshore (Epstein 1971).

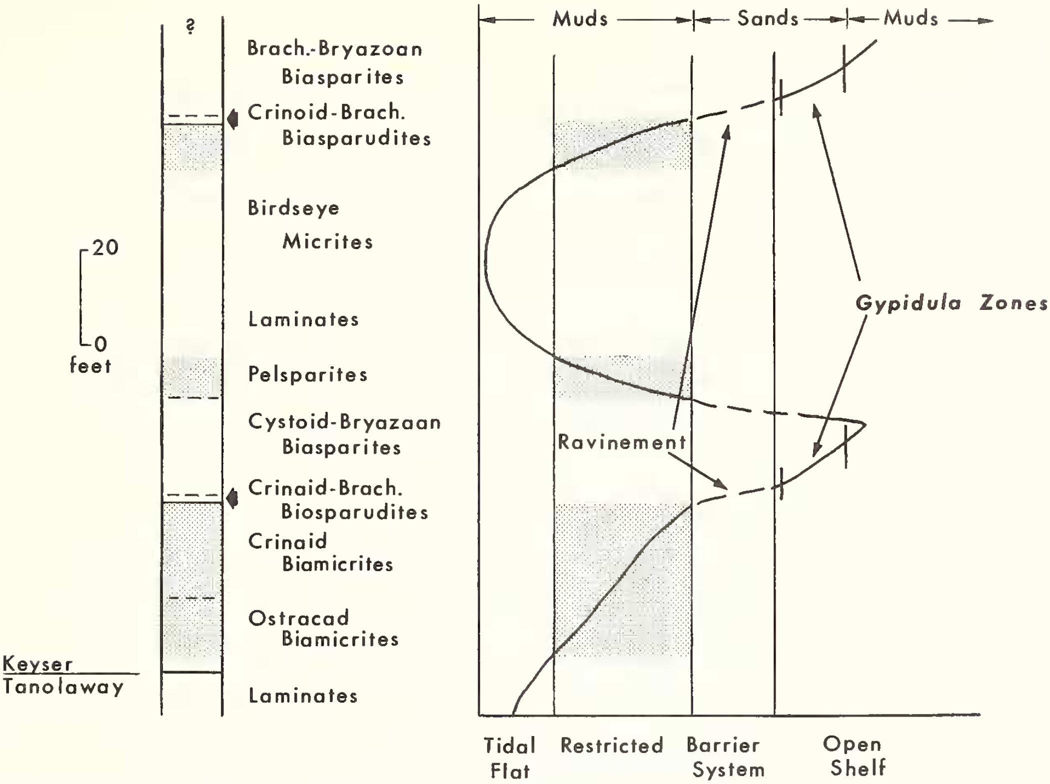
PALAEOENVIRONMENTAL EVIDENCE

Vertical sequences (*Upper Silurian*). Gypidulid brachiopods occur only at one position in vertical and lateral facies sequences in the Appalachian Basin. General stratigraphic relationships are depicted in text-fig. 2. In the Pennsylvania–Virginia



TEXT-FIG. 2. Stratigraphic cross-sections of Upper Silurian and Lower Devonian formations in the Appalachian Basin keyed to locality numbers in text-fig. 1. The section on the left extends from Syracuse (nearshore) to Albany (basin axis). Thicknesses are measured from a time datum in the upper Manlius (Rickard 1962).

The section on the right approximately parallels the basin axis from central Pennsylvania to Monterey, Virginia. Thicknesses are measured from a time datum in the middle Keyser (Head 1969) approximately coincident with the *Gypidula prognostica* epibole (the upper gypidulid occurrence). Sedimentation is continuous across the Silurian–Devonian boundary which is placed within the bracketed interval (Head 1969; Bowen 1967; Rickard 1962). Correlative transgressive events are marked by arrows. The gypidulid-bearing slabs (Pls. 39, 40) came from locality 87 (Sharon Springs, N.Y.) and locality 5 (Hyndman, Pa.).



TEXT-FIG. 3. Detailed columnar section and environmental interpretation of the lower half of the Keyser Formation at locality 5, Hyndman, Pa. Gypidulids are narrowly restricted to transgressive sand-grade open-shelf environments.

area the sequence of formations, Tonoloway–Keyser–New Creek–New Scotland, represents basinal transgression from tidal flats to fossiliferous shelf muds (Head 1969).

Within the Upper Silurian Keyser Formation, a more specific environmental sequence can be detailed. Two transgressions each terminated by progradation are recorded at widely separated localities. Gypidulid brachiopods occur at two specific horizons within these environmental sequences. This is well illustrated in the Keyser Formation at Hyndman, Pennsylvania (text-fig. 3).

The vertical sequence of lithologies (facies) at Hyndman is depicted in the measured column in text-fig. 3. The sequence: laminites, ostracod-crinoid biomicrite, brachiopod-crinoid calcarenite, to brachiopod-bryozoan-cystoid calcisiltite represents the first transgressive sequence. An erosional loss of high-energy barrier deposits may occur at the centre of the sequence which is interpreted as a ravinement (Swift 1968).

The above sequence is followed in order by: brachiopod-pelletal calcisiltites, laminites, and birdseye filled micrites representing the infilling of onshore subtidal zones and tidal flat progradation. Gypidulids are not present in this sequence. The transgressive sequence is then repeated with preservation of a massive bed of gypidulids in the brachiopod-crinoid calcarenite position (Pl. 40, figs. 1–3, 6). At Hyndman *G. prognostica* occurs only at this one level. In the Keyser Formation at nearby localities the species also occurs in the lower brachiopod-crinoid facies. The upper Keyser again progrades to tidal flats before transgression is re-established with the New Creek Formation, a brachiopod-crinoid calcarenite, which again contains gypidulids (*G. coeymanensis*).

Lateral sequences (*Lower Devonian*). The stratigraphic sequence in New York State is analogous to that in the Pennsylvania–Virginia region. It begins with deposition of very restricted sediments in the Rondout Formation and proceeds to deposition of offshore fossiliferous sediments, the New Scotland Formation. The sequence includes several episodes of progradation and it is possible to match some of these cyclic events with those occurring to the south (text-fig. 2).

Anderson (1971*a*) has established a lateral sequence of environments within the Coeymans Formation, a brachiopod-crinoid calcarenite. During transgressive or stable shoreline periods the lateral sequence is: 1, barrier deposits; 2, shallow stratified bar calcarenites; 3, bioturbated calcarenites deposited a little above wave base (Anderson 1972). These occur within the general sequence outlined above (text-fig. 4). *G. coeymanensis* occurs only offshore from the barriers, a little above wave base. Samples oriented in life position have been found at this position in the lateral facies sequence at several localities in the Coeymans Formation.

At most localities gypidulid-bearing, biogenically disrupted shelf sands overlie onshore restricted sediments (Manlius Formation) with a ravinement contact in vertical section. As in the Hyndman section, barrier deposits are removed by the ravinement process (Anderson 1972). During progradation of the Manlius tongue gypidulids disappear in adjacent Coeymans facies.

Community patterns. Ziegler (1965) has identified a recurrent pattern of communities (*Lingula* through *Clorinda* Communities) which sequentially occupy zones parallel to shore. Ziegler's central community, the *Pentamerus* Community, is directly analogous to *Gypidula* and its associated faunal assemblage. *Gypidula* has a similar shape and orientation mechanism to *Pentamerus* (Ziegler *et al.* 1966) and is associated with a limited brachiopod assemblage of similar robust forms. It also occupies an analogous position in an onshore to offshore sequence of communities based on form, diversity, and key related genera (Anderson 1971*b*). The evidence from gypidulids indicates that the distribution of the '*Pentamerus* Community' is controlled by sedimentary environment, specifically substrate type, and salinity.

EXPLANATION OF PLATE 40

Figs. 1–3. Upper Silurian, Hyndman, Pa. (loc. 5). Three views of the bottom surface of a large slab containing *G. prognostica* in life position. 1, ×2, 2, ×1·5, 3, ×1·8.

Figs. 4, 5. Negative prints of thin sections. Gypidulids in a poorly sorted sand to mud-size substrate, the Coeymans Formation, Sharon Springs, N.Y. (loc. 87), bar scale 3 mm. 4, Longitudinal cross-section through both valves of an articulated gypidulid in life orientation on its original substrate. ×2·5. 5, Transverse cross-section of a pedicle valve near the beak showing thick shell and median septum. ×3.

Fig. 6. Negative print of thin section, bar scale 3 mm. Disarticulated but unbroken gypidulid pedicle valve in association with a typical substrate, the Keyser Formation, Hyndman, Pa. (loc. 5). The inner prismatic layer thickens the posterior end of all pedicle valves. ×3.


1


2


3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5


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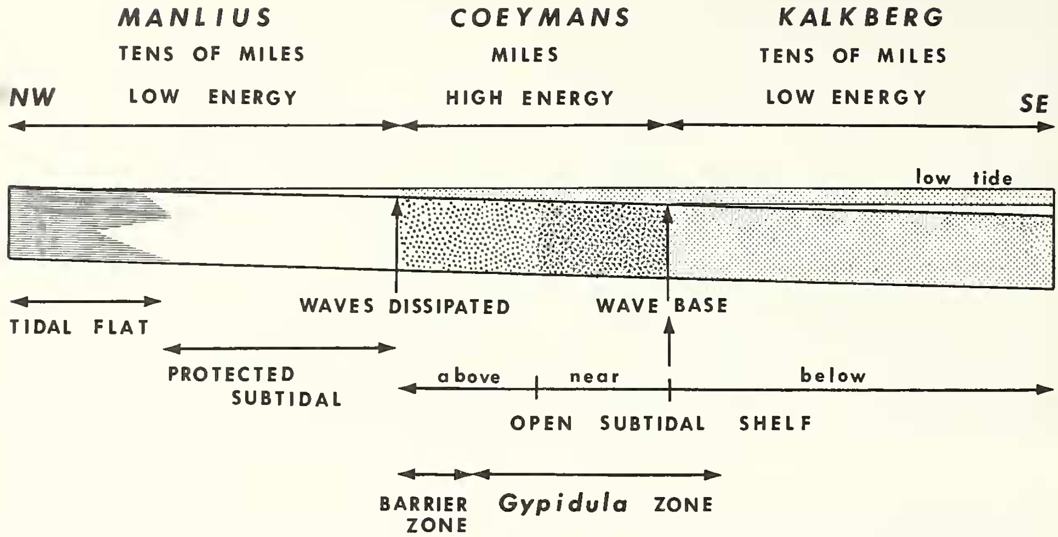

TEXT-FIG. 4. Idealized cross-section relating contemporaneous lower Helderberg formations to depositional environments from the basin margin to the basin axis. The distribution of kinetic energy, barrier development, and gypidulids are indicated. The zone of sand-grade deposition is narrow relative to onshore and offshore zones of mud deposition.

Environment. Gypidulids are adapted by their weighting mechanism for slowly shifting sand-grade substrates, an environment in which fixed attachment points are not available. Sediments which average in the sand-size range are interpreted as wave or current reworked deposits. However, biogenic disruption and abundant silt and clay-sized particles in the sand suggest a non-persistent physical reworking. In addition most brachiopods are adapted for life in water with good circulation, normal salinity, and low rates of sediment accumulation. All the above conditions probably prevailed on the open shelf, a little above wave base, in middle Palaeozoic epeiric seas.

The occurrence of gypidulids at two stratigraphic levels in the Keyser Formation and two levels in the Coeymans Formation, each occurrence corresponding to this one environmental position on the open shelf, confirms this interpretation. This environmental position can be identified in both vertical and lateral facies sequences. The lateral facies evidence places the gypidulid fauna offshore from a high-energy or barrier zone. The vertical facies evidence places the fauna in a transgressive sequence offshore from an interpreted barrier indicated by a ravinement.

The transgressive setting, although not necessary, provides an optimum environment for the gypidulid fauna. A landward migrating barrier system, believed to be typical of a transgressing epeiric sea, leaves behind a well reworked shelf sand (Anderson 1972). Shelf sedimentation rates would be relatively low and the barrier system would protect nearshore shelf communities from fluctuating salinities and influxes of mud from restricted onshore zones. Progradation in the Keyser and Coeymans Formations is correlated with the disappearance of gypidulids, apparent loss of barrier systems, more rapid sediment accumulation, and less reworking.

CONCLUSIONS

Gypidulid brachiopods discovered in their life orientation indicate that they are specialized for extensively reworked yet poorly sorted sand substrates. Recurrent appearance at one position in vertical and lateral facies sequences, that is in open shelf sediments near wave base, indicates that gypidulids were specific to this environment. Identification of the *Gypidula* fauna as equivalent to a *Pentamerus* Community suggests similar environmental controls (primarily substrate and salinity for Ziegler's community). A gypidulid fauna is most likely to develop in a transgressing epeiric sea where optimum substrate and salinity conditions occur in the shallow near wave base zone.

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E. J. ANDERSON

Department of Geology
Temple University
Philadelphia, Pennsylvania 19122

J. H. MAKURATH

Department of Earth and Planetary Sciences
The John Hopkins University
Baltimore, Maryland 21218
U.S.A.

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